

THE XEROPHILOUS CHARACTERS OF *HAKEA*
DACTYLOIDES Cav. [N.O. PROTEACEÆ].

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(Plates ix.-x.)

Hakea dactyloides is a low shrub, very common in sandy places about Sydney, and on the coast and mountains wherever the Hawkesbury Sandstone occurs. It is associated with *Petrophila pedunculata*, *Banksia ericifolia*, *B. serrata*, *Lambertia formosa*, *Hakea pugioniformis*, *Leptospermum scoparium*, *Darwinia fascicularis* and other xerophytes.

Like all drought-resisting plants, it is of slow growth, and the stems are tough and woody. They are covered with hairs of two kinds, long and slender, and capitate hairs of small size. The vascular bundles contain many thick-walled fibres, which make the twigs very tough.

The leaves are rather few in number, arranged spirally, and placed vertically, so that the edges are presented to the light. They are obovate in shape, narrowing to a short petiole. The apex of the leaf is sometimes quite rounded (*a*, Fig. 1), and sometimes narrowing to a short point (*b*, Fig. 1). In the latter variety, they are relatively rather narrower than the round-topped leaves are. There are three principal veins, the secondary veins ramifying in between, and these sometimes have blind ends (Fig. 1). There is also a vein round the edge. They vary in size according to the character of the season in which they develop. If the growth period—November to February—be wet, they reach a size of 14×3.5 cm.; if rain is scarce, they barely reach 6×1.5 cm. They are thick, rigid, and tough. The colour is light olive-green (darker in plants growing in shady places), with the marginal thickening reddish. The surface is smooth and dull, and the primary veins project on both sides. The young leaves and shoots have a dense

vestiture of hairs, those on the outside being a beautiful golden-brown, and those beneath silvery. They are spindle-shaped and thick-walled (Fig. 2). They fall off soon after the leaf has reached full size.

The stomates are found on both sides. They are sunk beneath the surface, and open into a vestibule formed by an upward arching of the surrounding epidermal cells, the aperture being at one end of the chamber, and directed towards the apex of the leaf. The chamber is 0.06 mm. long, 0.04 mm. wide, and the aperture 0.01 mm. in diameter. The stomata are numerous, as many as 120 to the square millimètre, making about 120,000 to an average-sized leaf. The epidermal cells are small, 0.01 mm., and rounded in form.

Seen in transverse section, the epidermis is composed of small cells, about 0.005 mm. high. The cuticle is very thick, 0.015 mm. (Fig. 3), of a dull olive-brown colour after the rest of the leaf has been decolorised by spirit. The cells are usually empty, but now and then contain cubical crystals. Scattered about in the epidermis are found capitate hairs in sunken cavities (Figs. 6-7). In the young leaf, these hairs are more plentiful. The interior wall of the epidermis projects downwards into the palisade tissue (Fig. 6*a*). The hairs are thick-walled, and apparently empty; but the cavity stains with saffranin or gossypimin very deeply.

In the young leaf, the hairs project above the surface of the epidermis, and apparently as the leaf gets older, the cuticle grows up, so as to surround the hairs. Many of the hairs drop off while the leaf is young, and the portions of the epidermis, on which they were seated, grow up to the level of the rest, leaving no trace of the former existence of the hairs.

The mesophyll consists of palisade cells in two layers under each face of the leaf. The cells are rather large, 0.06 mm. long, and 0.0075 mm. wide, packed with rather large granular chloroplasts. There are no intercellular spaces, except just under the stomata (Fig. 5). Between the two layers of palisade cells, the mesophyll consists of irregularly rounded cells, containing chlorophyll, and measuring 0.04 to 0.06 mm. in diameter. There are no intercellular

spaces here either. These cells do not contain so much chlorophyll as the palisade cells.

All through the mesophyll are numbers of large scleroblasts or stone-cells, columnar and simple (Fig. 8), or massive and irregularly branched in all directions (Fig. 9). Occasionally, a detached cell is found among the palisade cells, but the greater number have one or more of their branches touching the inner wall of the epidermis, and this part is usually expanded as if it were soft, and pressing against the epidermis. The greatest axis of these cells is at right angles to the plane of the leaf. They only rarely pass into the central region of the mesophyll, and still more rarely extend through from one palisade layer to the other. In some of them, a central cavity is seen, very narrow and branching, but the branches do not always correspond to the arms of the cell (Figs. 8 and 9 *a*). There are also narrow openings in the thickened wall, leading straight in to the central cavity.

The vascular bundles have a very strong development of hard bast—sclerenchymatous fibres with thick walls and small lumina. The few spiral vessels and sieve-tubes are embedded in the centre of this. In the marginal vein, the fibres lie outside the veins, but not inside.

The foregoing description applies to mature leaves growing in the open. Plants growing in shady places show marked differences. The leaves of the plants in the open average 0.4 mm. in thickness, while those of shade-plants are only 0.3 mm. The following table shows the main differences in measurements between ordinary and shade-leaves.

	Ordinary leaf.	Shade-leaf.
Leaf, thickness	0.4 mm.	0.3 mm.
Epidermis, thickness...	0.04 mm.	0.01 mm.
Cuticle, thickness	0.015 mm.	0.005 mm.
Palisade cells, length	0.05 mm.	0.03 mm.

In the shade-leaves, each cell of the epidermis almost always contains a single cubical crystal. The stomates are fewer in number

than in the ordinary leaf, and the vestibules are shallow and wider. The palisade tissue is not so close, and is composed of shorter and narrower cells. The cuticle has not the brown tint of that in the ordinary leaf, being quite clear and transparent. The capitate hairs occur very sparsely. The scleroblasts are also rare. There is little difference in the external characters, except that the leaves of shade-plants have much darker green leaves, which may be accounted for by the thinness of the cuticle, and the absence of brown colour from it.

There can be no doubt but that the thick cuticle is a powerful factor in checking transpiration and this is aided by the deeply sunken stomates. The closeness of the palisade cells and the absence of intercellular spaces also aid in this. The young leaf is effectively protected by the thick coating of hairs.

The most remarkable feature of the leaf is the great development of scleroblasts. In the young leaf, even up to the time when it has reached full size, there are none to be found; and we have seen that, in those growing in the shade, they are rare or absent. But as the mature leaf, exposed to sun and wind, grows older, small masses of sclerenchyma appear in the middle region of the leaf; these increase in size and number till they occupy a very large part of the mid-region of the leaf—as much, I estimate, as 45 % of it. They begin their growth among the palisade cells, and extend gradually outwards till they reach the epidermis, and then the part touching the epidermis extends laterally. As to their origin, it is most likely, as Sachs conjectures, that they are nothing more than peculiarly developed parenchyma cells(1,p.146). From the fact that they develop most in leaves exposed to intense light, heat, and wind, it would appear that their occurrence is a direct consequence of those conditions. Their function is probably the same as that of the closeness of the mesophyll, viz., diminishing transpiration by, as Sachs states (1,p.144), slowing the exchange of sap between the parenchymatous tissue and the veins.

The function of the sclerenchymatous fibres round the vascular bundles is apparently to give rigidity to the leaf, but they would also undoubtedly assist in slowing transpiration, as they are always

very strongly developed in plants exposed to dry conditions, and particularly so in the Proteaceæ(2). That they are effective in enabling the plant to withstand the effects of a dry environment, may be inferred from their common occurrence in such conditions in plants of very diverse natural orders.

REFERENCES TO LITERATURE.

- (1) SACHS, On the Physiology of Plants.
 (2) HAMILTON, "On the structure of the leaf in *Banksia serrata*," Report Aust. Assoc. Adv. Sc. 1907.
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EXPLANATION OF PLATES IX.-X.

Plate ix.

- Fig.1.—Venation of leaf, ($\times \frac{1}{2}$).
 Fig.2.—Hairs on young leaf.
 Fig.3.—Epidermis and one row of palisade cells of ordinary leaf; *c*, cuticle.
 Fig.4.—Epidermis and one row of palisade cells of shade-leaf; *c*, cuticle.
 Fig.5.—Section of stomate and vestibule; *v*, vestibule; *g*, guardcells.
 Fig.6.—Capitate hair in cavity; *a*, projection of epidermis into mesophyll.
 Fig.7.—Ditto.
 Fig.8.—Simple scleroblasts; *a*, cavity.
 Fig.9.—Massive, branched scleroblasts; *a*, cavity.

Plate x.—Microphotographs.

- Fig.10.—Cross-section of ordinary leaf; *c*, cuticle; *s*, scleroblasts.
 Fig.11.—Cross-section of shade-leaf; *c*, cuticle; *s*, scleroblasts.
 Fig.12.—Section parallel to plane of leaf; *s*, scleroblasts cut at right angles.